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Archaeogaia macachaae gen. et sp. nov., one of the oldest Notoungulata Roth, 1903 from the early-middle Paleocene Mealla Formation (Central Andes, Argentina) with insights into the Paleocene-Eocene South American biochronology

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Abstract

In this contribution, we report the discovery of *Archaeogaia macachaae* gen. *et* sp. nov., one of the oldest notoungulate recovered from the upper section of Mealla Formation in the Tonco Valley (Northwestern Argentina, Salta Province). The new material consists on a left mandibular fragment with damaged m1 and complete m2-3. *Archaeogaia macachaae* is characterized by the following combination of features: m1 slightly shorter than m2 and both larger than m3; brachydont molars; talonid mesio-distally shorter than trigonid; metaconid slightly taller than protoconid and distally placed; reduced paraconid in m2; metalophid straight in m2–3, but it runs mesially forming a slightly obtuse angle in the labial edge in m2, whereas it is more transverse in m3; transverse entolophid; mesial cingulid extending from the middle to the lingual face of molars; and distal cingulid connecting the hypoconulid with the mesial face of the entoconid on m2–3. We perform a phylogenetic analysis based on a data matrix composed of 147 craniodental characters and 70 taxa. The analysis yields 6104 most parsimonious trees of 423 steps each. In the strict consensus previously well-supported clades collapse into a polytomy; and *Archaeogaia* is positioned within the order Notoungulata based on two synapomorphies: a) presence of a transverse entolophid, and b) lower cheek teeth with short mesio-distal protolophid, transverse metalophid and mesio-distal hypolophid slightly convex labially. The former character was recovered as a synapomorphy for Notoungulata in several previous studies. According to the reduced consensus, *Archaeogaia* occupies different positions within the order; these fluctuating locations could be the result of the presence of plesiomorphic features in the holotype, and the absence of the structures that define the notoungulate clades in which the new taxon is located. The paleomagnetic data indicates that the Mealla Formation was deposited during Chron 27r to the base of Chron 26r (latest Danian-earliest Selandian). In this context, we discuss the

finding of *Archaeogaia*, and the age of Mealla Formation in the South American biochronology.

Keywords. South American native ungulates. Peligran. Tiupampan. Riochican. Northwestern Argentina.

I. Introduction

Order Notoungulata (Roth 1903) is considered the most diverse clade of the South American native ungulates (SANUs) in reference to its taxonomy, morphology, and ecology (Croft et al., 2020). The members of this order were well-distributed throughout South America during most of the Cenozoic. The notoungulates reached North America in the Pleistocene during the Great American Biotic Interchange (Woodburne, 2010; Croft et al., 2020). Currently, there is no record of this order in Antarctica, the reason why their southern distribution was assumed to be confined to Patagonia (see Madden et al., 2010).

The older undoubted Notoungulata were found in the early-middle Paleocene of the Central Andes of Argentina and Bolivia (Pascual et al., 1978; Muizon, 1991). These records are conformed by the henricosborniid genus *Simpsonotus* from the Mealla Formation (Fm.), Northwestern Argentina (Pascual et al., 1978), and a henricosborniid from Bolivia (Muizon, 1991; Muizon et al., 2019). Notoungulates from the Paleocene-Eocene transition are represented by *Perutherium* from the Laguna Umayo local fauna, whose most reliable age is late Paleocene-early Eocene in age (Sigé et al., 2004 but see Chornogubsky and Goin, 2015 for an ancient age). Similarly, the Río Loro Fm. from Tucumán Province, where *Satshatemnus* Soria and Powell, 1981) is considered alternatively as middle Paleocene or early Eocene (Gelfo et al., 2020). During the early Eocene, the record shows an increase in the taxonomical diversity, concomitant with an expansion of the geographic distribution of the taxa. In the Itaboraí Quarry (Brazil), the henricosborniid *Camargomendesia*, and the

oldfieldthomasiids *Colbertia* and *Itaboraitherium* were exhumed (Bond et al., 1995). In Patagonia, notoungulates were registered for the first time in the *Kibenikhoria* faunal zone (Simpson, 1935), which currently corresponds to the lower and middle levels of Las Flores Fm. (Krause et al., 2017). In this unit, and in addition to the oldfieldthomasiid *Kibenikhoria*, the record includes the henricosborniid genera *Othnielmarshia*, *Henricosbornia*, *Perypantostylops*, and *Orome* (Woodburne et al., 2014; Bauzá et al., 2019), and the archaeopitheciid *Teratopithecus* (López et al., 2020).

Recent molecular evidence supports a close relationship between Notoungulata + Litopterna and Perissodactyla (Welker et al., 2015; Westbury et al., 2017). This was reflected in the erection of the unranked taxon named Panperissodactyla in order to include these taxa. The split between the clade Notoungulata + Litopterna and Perissodactyla was estimated around 88-73 Ma. by Welker et al. (2015) and in ~66 Ma. by Westbury et al. (2017). The divergence of Notoungulata and Litopterna was estimated in ~69-64 Ma. (Welker et al., 2015), but Westbury et al. (2017) suggested that this event took place immediately after the K-Pg boundary (~66 Ma). In this context, the early Paleocene is a time of great importance for the evolution of the SANUs.

In this contribution, we present a new mammalian monospecific genus recovered from the early-middle Paleocene strata of the Mealla Fm., Salta Province, Argentina. This novel taxon, together with *Simpsonotus* spp., represents the oldest record of the order Notoungulata. We tested the phylogenetic relationships of this new taxon in the context of the SANUs, and discussed its relevance for the biochronology of South America.

II. Geological settings of the study area

The Salta Group is formally divided into three subgroups: Pirgua (Lower Cretaceous), Balbuena (Upper Cretaceous to early Paleocene), and Santa Bárbara (early Paleocene to

Eocene). The Balbuena subgroup is composed, from the base to the top, by the Lecho, Yacoraite, and Tunal/Olmedo formations, while the Santa Barbara subgroup is conformed by the Mealla, Maíz Gordo, and Lumbrera formations (Salfity and Marquillas, 1994).

In the Tonco Valley (Figure 1A), the average thickness of the Mealla Fm. is about 160 m. It is characterized by red to purple colored deposits that clearly distinguishes it from the underlying Yacoraite and the overlying Maíz Gordo formations, with which it is in paraconformable contact (Palma, 1984; Quattrochio et al., 1997). The Mealla Fm. consists on medium-grained sandstone levels with erosive bases deposited in an anastomosed to a braided fluvial system (Palma, 1984) (Figure 1B). The fossil remain presented here was recovered from the 10 m below the contact with Maíz Gordo Fm. (Figure 1B). The paleoenvironmental reconstruction of the Mealla Fm. suggests an extensive fluvial plain temporarily flooded, with perennially active sinuous channels draining that plain (Palma, 1984). On the top of the unit, the 'Faja Gris' (not preserved in the area of study) carries a Selandian palynomorphs assemblage that allowed infer a paleoenvironment characterized by humid tropical to intertropical forest with episodes of seasonal dryness (Quattrochio et al., 1997; Marquillas et al., 2005).

[Insert Figure 1 about here]

The age of the Salta Group is constrained by absolute dates measured in the middle and the top of the section (Marquillas et al., 2011) (Figure 2). The Yacoraite Fm. has been dated with U-Pb zircon age of 68.4 ± 0.7 Ma based on a tuff level 49 m below the top of the unit. The upper boundary of the Salta Group was dated on 39.9 Ma (del Papa et al,. 2010) based on a tuff bed from the upper levels of Lumbrera Fm. Recent paleomagnetic studies contributed to increase the age resolution of the intermediate units (Hyland et al., 2015; 2017; Hyland and Sheldon, 2018). Hyland et al. (2015) constructed a geomagnetic polarity column involving the Tunal/Olmedo-Maíz Gordo section (Figure 1B). These authors used the

palynological zonation of Quattrochio et al. (1997) and Quattrochio and Volkheimer (2000) to set a Danian age for the Tunal/Olmedo Fm. and the Selandian age of the Mealla Fm. (Hyland et al., 2015:374). However, the authors erroneously located the Selandian palynozone of the Mealla Fm. in the base of the unit, even though the palynoflora was recorded in the 'Faja Gris', which constitutes the top of the unit (Quattrochio and Volkheimer, 2000:354). This interpretation impacted on the correlation of the magnetozones with the geomagnetic polarity time scale (GPTS) and, consequently, on the age model presented by Hyland et al. (2015), thus, interpreting the sequence as younger than it really is. The Mealla Fm. presents, from base to top, one reversal, one normal, and another reversal polarity intervals (Hyland et al., 2015: fig. 3). Considering that the Selandian age given by the palynoflora provided an age constraint for the top of the unit, the most parsimonious correlation of the three polarity intervals within the Mealla Fm. is Chron 27r- 27n-26r. Then, the Mealla Fm. sedimentation should extend from the late Danian to the Selandian. Similar critics to the age model of Hyland et al. (2015) and subsequent publications (Hyland et al., 2017; Hyland and Sheldon, 2018) were made by White et al. (2018), who re-interpreted the magnetostratigraphic correlations of Hyland´s models. White et al. (2018) proposed that the normal interval in the Tunal/Olmedo Fm. is correlated with Chron 28n and the normal polarity interval of Mealla Fm. is correlated with Chron 27n (Figure 2B). The age of the Mealla Fm. is then constrained between Chron 27r to 26r (63.49-59.23 Ma; Ogg, 2012).

Historically, the Mealla Fm. has been correlated with levels of the Río Chico Group (Pascual et al., 1981) and the Banco Negro Inferior (BNI) of the Salamanca Fm. (Marshall et al., 1997) in Chubut Province, and with the Santa Lucía Fm. (Marshall et al., 1997; Marquillas et al., 2011) in Bolivia. In the current stratigraphic arrangement of the Río Chico Group (Raigemborn et al., 2010; Raigemborn and Beilinson, 2020), the only possible correlation of the Mealla Fm. is with the base of this group, which is composed by Las

Violetas and Peñas Coloradas formations (Raigemborn and Beilinson, 2020). The latter is correlated with the interval polarity Chrons 27n-26r (Clyde et al., 2014). The BNI is correlated with Chron 28n based on isotopic dates, magnetostratigraphy palynology, foraminiferal, nannofossil contents, sequential stratigraphy, sedimentary analysis, mineralogy, and hydrological proxies (Clyde et al., 2014; Comer et al., 2015; Raigemborn and Beilinson, 2020). In this sense, its correlation with the Mealla Fm. is discarded because it is older. Finally, the deposition of the Santa Lucía Fm. is considered correlated to Chron 26r by isotopic dates, magnetostratigraphy, vulcanism, eustasy, and paleontological content (Sempere et al., 1997), structural analysis (De Celles and Horton, 2003; Calle et al., 2018; Horton, 2018), plutonism (Demouy et al., 2012), and thermochronology (Rak et al., 2017). Due to the fact that the Mealla Fm. extends from Chron 27r to Chron 26r, only a portion of this unit is potentially equivalent to the Santa Lucía Fm.

[Insert Figure 2 about here]

III. Material and methods

3.1 Taxonomic analysis

The specimen studied here is currently stored in the Paleontological Collection at the Instituto de Bio y Geociencias del Noroeste Argentino (IBIGEO-P), Rosario de Lerma, Salta Province, Argentina. The following materials and bibliography were used as comparative purposes: *Simpsonotus praecursor* (MLP 73-VII-3-11; Pascual *et al.* 1978), *S. major* (MLP 73-VII-3-12; Pascual et al., 1978); *Peripantostylops minutus* (MACN-A 10711; Ameghino, 1901; Simpson, 1948); *Itaboraitherium* (calcotype MACN-PV 18872; and cast MACN -PV 18873); *Colbertia magellanica* (Price and Paula Couto, 1950; 1952; Cifelli, 1983); *C. lumbrerense* (PVL 4607, PVL 4183, PVL 4184, PVL 6218; Bond, 1981; García-López, 2011); *Othnielmarshia* (MACN-A 10807; Ameghino, 1901; Paula Couto, 1978)*; Henricosbornia lophodonta* (MACN-A 10802, MACN-A 10808, MACN-A 10716, MACN-A 10717,

MACN-A 10792. MACN-A 10795, MACN-A 10796, MACN-A 10809; Ameghino, 1901; Simpson, 1948); and *Dolychostylodon* (García-López and Powell, 2009).

All the nomenclatural acts follow the regulations established by the ICZN (2000). The dental terminology mainly follows the nomenclature proposed by Simpson (1967), Hooker (1986) and Vera (2012). The measurements indicated in this contribution were taken with a Vernier digital calliper (+/- 0.001 mm). The photographs were taken with AxioCam ERc5s camera coupled to a Zeiss Stemi 305 stereomicroscope.

3.2 Phylogenetic analysis

A phylogenetic analysis was carried out in order to evaluate the phylogenetic relationships of the new genus in the context of the Notoungulata and the SANUs as well. The data matrix used here is the one published by Deraco and García-López (2016), which was in turn modified from Billet and Muizon (2013). This is the most complete data matrix in regards to notoungulates sampling, and it includes four of the five SANUs groups. It is worth mention that we have decided not to use the data matrix of Muizon et al. (2015), which includes an important representation of mammals, but in terms of the SANUs it presents the same representatives of Litopterna, Pyrotheria, and Astrapotheria, much less of Notoungulata, and only incorporates one Xenungulata when comparing to Deraco and García-López (2016). In addition, this last analysis resolves better the relationships at the SANUs level. In order to include all SANUs in our analysis, we have incorporated the Xenungulata *Carodnia* into the data matrix. A new diagnostic dental character of the new taxon was added to the data matrix (ch. 147): 'Lingual cingulid running mesially from the hypoconulid to the mesial face of the entoconid (0) absent; (1) present'. A total of 147 discrete cranial and dental morphological characters were scored in 70 taxa. Following Deraco and García-López (2016), ten characters were treated as ordered, and all characters were equally weighted (see Supp. Data1). A new technology search was performed with TNT

1.5 software (Goloboff and Catalano, 2016) because this kind searching strategy is more effective than traditional searches when working with large data sets (Goloboff, 1999), using initially the combination of Sectorial Searches (SS) and Tree fusing (TF) algorithms, obtaining trees through a directed search hitting the optimal 100 times, and finally using a the tree bisection reconnection algorithm with 100 replications retaining 10 trees per replication. Strict and reduced consensuses were calculated. The latter was considered due to ambiguity caused by the highly unstable position of the new taxon (Wilkinson, 1994; 1995; 2001); this method allows avoiding the ambiguity inherent in the polytomies of the strict consensus tree by selectively pruning or removing branches that constitute those polytomies (Wilkinson, 1994). On the other hand, branch support values were estimated by Bremer (see Bremer, 1994), and Bootstrap (absolute and GC frequencies) indices using TNT 1.5.

3.3 Abbreviations

Institutional Abbreviations. **IBIGEO**, Instituto de Bio y Geociencias del Noroeste Argentino; **MACN-A**, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'-Ameghino National Collection, Buenos Aires, Argentina; **MACN-PV**, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia´-Vertebrate Paleontology Collection, Buenos Aires, Argentina; **MLP**, Museo La Plata, La Plata, Argentina.

Anatomical Abbreviations. **C/c**, upper/lower canine; **I/i**, upper/lower incisor; **L**, length; **M/m**, upper/lower molar; **P/p**, upper/lower premolar; **W**, width.

Other Abbreviations. **Ma**, *megannum*, one million years in the radioisotopic time scale; **MPTs**, most parsimonious trees; **NALMA,** North American Land Mammal Age; **SALMA**, South American Land Mammal Age; **SANUs**, South American native ungulates.

3.4 Definitions. The Tunal Fm. is the surface equivalent of the Olmedo Fm. (Moreno, 1970) originally defined on the base of the subsoil profiles, which are thicker than the Tunal Fm.

outcrops. The levels of the Tunal Fm. are equivalent to the final cycle in the deposition of the Olmedo Fm. (Stark, 2011).

The Lumbrera Fm. was defined by Moreno (1970), and informally divided into three sections (Gomez Omil et al., 1989; Marquillas et al., 2005) or two section (del Papa et al., 2006; 2010). Here, we follow the latter proposal because it is more extended in the paleontological literature and, at the moment, there is not a formal definition of the upper and lower sections as individual formations.

IV. Systematic Paleontology

PANPERISSODACTYLA Welker et al., 2015

Order NOTOUNGULATA Roth, 1903

Family Incertae sedis

Archaeogaia gen. nov.

Type species. Archaeogaia macachaae

Derivation of name. Dedicated to Gaia, the ancestral mother of all life and the primal Mother Earth goddess according to Greek mythology; and —*Archaeo* means ‘primitive’ in Greek.

Diagnosis. Very small and brachydont notoungulate, characterized by the following combination of features: m1 slightly shorter than m2 and both larger than m3; talonid slightly shorter than trigonid; metaconid slightly higher than protoconid and distally placed; paraconid in the m2 reduced to a small cusp fused to the mesio-lingual wall of the metalophid; straight metalophid in the m2 which runs mesially forming a slightly obtuse angle in the labial edge with the longitudinal axis of the tooth which becomes more transverse in the m3; mesial cingulid extending from the middle to the lingual edge of

molars; transverse entolophid; strong distal cingulid running mesially from the hypoconulid to the mesial wall of the entoconid, which is particularly conspicuous in the m3.

Remarks. *Archaeogaia* presents a morphology resembling that of the basal notoungulates traditionally referred to the family Henricosborniidae. Considering these taxa, *Archaeogaia* differs from *Simpsonotus* by its less developed paraconid, more prominent protoconid, more lophodont cristid obliqua and entoconid, and the m3 shorter than the m2. It also differentiates from *Henricosbornia*, *Peripantostylops*, and *Othnielmarshia* by its more lophodont crests, less developed paraconid and cristid obliqua, less crescentic hypoconid, more lophoid entoconid, and shorter m3. It is similar in size to *Peripantostylops minutus*, but its m3 is smaller. From the 'Oldfieldthomasiidae' *Colbertia* and *Dolychostylodon*, *Archaeogaia* differs by its less developed paralophid and paraconid, trigonid higher than the talonid, less crescentic cristid obliqua and hypoconid, and more bunoid entoconid. *Archaeogaia* differentiates from the notoungulate (oldfieldthomasiid?) *Itaboraitherium* by its less expanded entoconid. *Archaeogaia* differs from all known Notoungulata in the presence of a distal cingulid extending mesially from the hypoconulid to mesial face of the entoconid. *Archaeogaia* shares the presence of a small paraconid fused to the mesio-lingual wall of the metalophid with *Dolychostylodon*, *Simpsonotus* and *Henricosbornia*.

Locality and Stratigraphic Context. Tonco Valley, Salta Province (Argentina), Mealla Formation, early-middle Paleocene.

[Insert Figure 3 about here]

Archaeogaia macachaae gen. et sp. nov.

(Figures 3–4)

Holotype. IBIGEO-P 73, left mandibular fragment with damaged m1 and complete m2–3.

Hypodigm. The holotype.

Derivation of name.—macachaae in honor to María Magdalena Dámasa Güemes de Tejada (1787-1866), known popularly as ‘Macacha’, patriot woman who lived in Salta and played a fundamental role in the independence of Argentina.

Measurements. Table 1

Diagnosis. As for the genus for monotypy.

Description. The molar series is brachydont and the m1 and m2 are approached in length with the latter slightly larger; the m3 is shorter than the other molars (see Table 1). The m1 is fractured along the ectoflexid and its lingual face is badly preserved so its measurements are approximated. The mesial face of the trigonid is concave, a fact that suggests that the p4 could probably have a hypoconulid distally placed and enclosed in this hypoconulid notch. The shape of the metalophid is not preserved due to the breakage of the trigonid. The cristid obliqua seems to join the metalophid in its middle point. Remains of a disto-lingual cingulid is preserved (Figure 3A).

The trigonid of the m2 is sub-quadrangular in outline; the metaconid is higher than the protoconid, and distally placed; the paralophid is short and slightly labially convex, being the less conspicuous lophid; the protoconid is wide and strong; the protolophid is slightly labially convex, and mesio-distally expanded; the metalophid is well-developed, straight, and runs mesially forming a slightly obtuse angle in the labial edge with the longitudinal axis of the tooth; the trigonid presents a very small and reduced accessory cuspid, which is inferred here as a paraconid, fused to the mesio-lingual wall of the metalophid; a low mesio-lingual cingulid runs from the mesio-lingual wall of the metalophid to the lingual portion of the paralophid; the cristid obliqua runs linguo-mesially merging with the labial half of the metalophid; the trigonid is shorter and higher than the talonid, but both present a similar width; the entoconid is distally placed in the talonid, well separated from the metalophid by the mesial talonid valley, and it is mesio-distally and transversally expanded forming a well-

developed entolophid, which is connected to the hypoconid region; the hypoconulid is small, but conspicuous, and it is located distal to the distal wall of the entolophid, separated from it by a shallow distal talonid valley; the hypolophid is lingually curved, and it is distally elongated; there is a slightly developed disto-lingual cingulid, which is low in the crown, and that runs mesially from the hypoconulid to almost the distal wall of the metaconid, surrounding the entoconid and connecting the mesial and distal talonid valleys, being thicker in the area between the hypoconulid and the entoconid; the ectoflexid is deep; and the talonid basin is shallow and wide (Figures 3A, B, 4A).

[Insert Figure 4 about here]

The m3 (Figures 3A, B, 4B) is quite similar to m2, but differs in exhibiting the following features: the trigonid is slightly wider than the talonid; the paralophid is less developed; the protolophid is less mesio-distally expanded, and more labially convex; the paraconid is more conspicuous, probably due to the less degree of wear of this molar; the metalophid is transverse, running lingually forming a right angle with the longitudinal axis of the tooth; the cristid obliqua contacts more labially, being much closer to the protoconid region; the ectoflexid is less deep; the hypolophid is longer, and less mesio-distally expanded; the distal talonid valley is more evident; the disto-lingual cingulid is more conspicuous especially on the entoconid region, but it is very feeble along the mesial talonid valley; and the talonid basin is more and less narrower.

Regarding the molar proportions, the m3 of *Archaeogaia macachaae* shows a reduction on its size. This tooth represents less than one third of the molar row length (Table 1). Despite m1 is slightly shorter than m2, the overall proportion of both teeth overpass the third of the total length (0.35).

4.2 Cladistic analysis

The cladistic analysis resulted in 6104 most parsimonious trees (MPTs) of 423 steps (CI=0.295; RI=0.650). Figure 5A shows the strict consensus with the support values for each node. Synapomorphies are listed in Appendix S2 (Supplementary Data). According to the results presented here, there is a basal tetrachotomy between *Zalambdalestes*, *Protolipterna*, the clade constituted by the representatives of stem Perissodactyla and Litopterna, and the clade Xenungulata + Astrapotheria + Notoungulata (Node 77; Figure 5A). In Node 77, the xenungulate *Carodnia* is the sister taxon of Node 76, which consists on the Astrapotheria as the sister taxon of Notoungulata (Node 78; Figure 5A). Notoungulata (Node 78) is recovered here as a monophyletic group. Our result shows a basal polytomy that includes *Archaeogaia*, *Pampatemnus, Boreastylops, Griphotherium, Notopithecus, Ultrapithecus, Acropithecus, Campanorco, Oldfieldthomasia, Colbertia, Rhyphodon, Periphragnis, Thomashuxleya, Pleurostylodon, Simpsonotus, Henricosbornia, Notostylops*, *Pyrotherium*, the remaining typotheres (Nodes 97 and 103), and toxodonts (Nodes 80 and 85) (Figure 5A). The Notoungulata clade is supported by two synapomorphies: lower cheek teeth with short mesio-distal protolophid, transverse metalophid and mesio-distal hypolophid slightly convex labially (54^1) and lower cheek teeth with entoconid transversely expanded into entolophid (55^1).

[Insert Figure 5 about here]

The inclusion of *Archaeogaia* changes the topology presented by Deraco and García-López´s (2016) as it failed to recover the main clades of Typotheria and Toxodontia well-supported in other analysis (Billet, 2011; Billet and Muizon, 2013; Deraco and García-López, 2016; Carrillo and Asher, 2017). The basal polytomy shown in the strict consensus (Node 78; Figure 5A) is associated with the different positions taken by *Archaeogaia* within Notoungulata in the MPTs; nevertheless, these results allow us to establish that *Archaeogaia* is a Notoungulata because it presents both synapomorphies mentioned above as

characterizing the order. The reduced consensus method allowed identifying the positions that *Archaeogaia* take within the MPTs (Figure 5B). It could be the sister taxon of Typotheria or could be nested within this clade as the sister taxon of (*Ultrapithecus Colbertia* (Interatheriidae)) or the Interatheriidae (Figure 5B). *Archaeogaia* could also be the sister taxon of Toxodontia, be nested within this clade as a basal 'Isotemnidae', or as the sister taxon of the clade constituted by Homalodotheriidae, Notohippidae, Toxodontidae, and Leontinidae (Figure 5B).

V. Discussion

5.1 Biochronology of the Mealla Formation

With the addition of *Archaeogaia*, the mammalian record of the Mealla Fm. consists of two genera and three species: *A. macachaae, Simpsonotus praecursor*, and *S. major*. This unit has been traditionally considered Riochican in age (Pascual et al., 1981; Gelfo et al., 2009). Pascual et al. (1978) considered *Simpsonotus* as an Henricosborniidae, a family with its first stratigraphic record in the levels described by Simpson (1935) as *Kibenikhoria* zone along the Río Chico in Chubut province. On this basis plus the lack of additional Casamayoran mammals, Pascual et al. (1978: 387) correlated the levels of the Mealla Fm. with the Riochican SALMA. However, since the original description of *Simpsonotus*, the South American biochronology has substantially changed and the Riochican SALMA went from being late Paleocene (Pascual et al., 1981) to middle Eocene in age (Woodburne et al., 2014; Krause et al., 2017). Most of these changes were promoted by the improved isotopic dates of the Río Chico Group. The word "Riochican" was established by Simpson (1933) in reference to the mammalian faunas recovered from the outcrops along the Río Chico course (Chubut province). Later, in 1935 the author considered that these beds involved three successive faunas, from oldest to youngest: *Carodnia*, *Kibenikhoria*, and *Ernestokokenia*

faunas (Simpson, 1935: 20). The author established the *Kibenikhoria* fauna as the 'typical Río Chico fauna' (Simpson, 1935: 16). It contained the most ancient remains of Notoungulata (Henricosborniidae and 'Oldfieldthomasiidae'), and it was considered older than the middle Paleocene (Simpson, 1935: 19). He also argued that the levels containing the *Ernestokokenia* faunal zone were immediately below the Casamayor levels at Bajo de la Palangana and could be a "proto-Casamayor or a transitional Rio Chico-Casamayor Fauna" (Simpson, 1935: 17). Later, Pascual (1965) established the Rio Chico fauna as the Riochican SALMA, but included all three faunal zones from Simpson (1935) in his concept. Since the SALMA was not linked to any locality or stratigraphic level, the timing of the first occurrence of the Notoungulata was lost in the broad sense of the Riochican. This view promoted that later authors (*e.g.*, Soria and Powell, 1981) proposed early and late Riochican stages. The 'typical Río Chico fauna' occurs in the strata currently corresponding to the Las Flores Fm. (Legarreta and Uliana, 1994). However, in the review of the stratigraphy of the Río Chico Group, Legarreta and Uliana (1994) anchored the Riochican SALMA to the Koluel-Kaike Fm. instead of Las Flores Fm. as in Simpson´s (1935) original model. Bond et al. (1995) maintained this stratigraphic arrangement and equated the Riochican SALMA to the *Ernestokokenia* faunal zone occurring in the Koluel-Kaike Fm. However, the Riochican SALMA was not redefined and the Pascual´s Riochican concept continued to be used (e.g. Gelfo et al. 2009). On this basis, the correlation of the Mealla Fm. with the Riochican SALMA was based on Pascual´s broad sense of the Riochican SALMA. This promoted that even in recent literature (e.g. Gelfo et al. 2009; Woodburne et al. 2014) the unit has been considered middle Eocene in age. However, we want to highlight here that given the new geochronological data provided for the Mealla Fm. (late Danian-early Selandian), the first record of an Henricosborniidae no longer corresponds to any of the levels of the Río Chico group but precisely to the Mealla Fm. (i.e. *Simpsonotus*). On this base it is evident the need of

a review and a redefinition of the SALMAs associated to the Río Chico group. In this context, we followed Krause et al. (2017) and used the Simpson´s faunal zones instead the Riochican SALMA (Fig. 2).

Until now, and posterior to the original publication of *Simpsonotus* spp., the oldest record of the order Notoungulata was an isolated and fragmentary upper molar assigned to the family Henricosborniidae (Muizon et al., 2919: 863), and recovered from the strata of the Santa Lucía Fm. at the Tiupampa locality in Bolivia (Muizon, 1991; Muizon et al., 2019). The age of this stratum was recently considered around 65 Ma (Chron 28r) by Muizon et al. (2019), based on Marshall et al. (1997), and Gelfo et al. (2009). The former reference is wrongly cited, because Marshall et al. (1997) placed the Tiupampan fauna in the Chron 26r. Regarding Gelfo et al. (2009), they made an effort to refine the relative age of Tiupampan fauna using two arguments. First, they suggested that the most primitive morphology of the Tiupampan pantodont *Alcidedorbignya inopinata* could indicate chronological antiquity when compared with the most ancient North American pantodons. The latter occurred in levels assigned to Chron27r. Second, these authors analyzed the faunal similarity between the Tiupampan SALMA, other Paleocene SALMAs, and the Puercan NALMA. They found that the Tiupampan SALMA shared one genus (‘*Peradectes’*) with the Puercan 3, an interval recorded in North America for chrons 29n and 28r. Then, based on the presence of ‘*Peradectes’* plus the primitiveness of *Alcidedorbignya*, Gelfo et al. (2009: p. 264) suggested that the reversed polarity at Tiupampa could be correlated to Chron 28r, thus corresponding to *Ca.* 65 Ma. Taking into account current hypotheses on the non-monophyletic nature of ‘*Peradectes’* (Williamson et al., 2012), the systematic relationships of the Tiupampa specimen assigned to this genus is uncertain. Thus, it is not possible to evaluate the true connection among South American ‘*Peradectes*’ and the ones from North America. In this sense, the only argument supporting the age of Chron 28r is the primitive morphology of

Alcidedorbignya. Nonetheless, the 'primitiveness' of the taxa present in the Tiupampan fauna could be explained by ecological factors, latitudinal effects or insularity (Ortíz-Jaureguizar et al., 1999; Pascual and Ortíz-Jaureguizar, 2007; Ortíz-Jaureguizar and Pascual, 2011), without the necessity to invoke the 'evolutionary state of taxa', especially when considering the large amount of recent geological evidence reinforcing the Sempere´s correlation of Santa Lucía beds with Chron 26r (e.g. Horton et al., 2001; DeCelles and Horton, 2003; Demouy et al., 2012; Rak et al., 2017; Calle et al., 2018). Moreover, it is surprising that Muizon et al. (2015; 2019) considered the 'suggested' correlation of the Tiupampan beds with Chron 28r by Gelfo et al. (2009) as a fact, then changing the correlation tool from faunal affinity analyses to a magnetic polarity approach, considering the Tiupampan SALMA as equivalent to the Torrejonian 1 NALMA (completely included in Chrons 29n-28r; Sprain et al., 2015).

5.2 Phylogenetic relationships and the early steps in the radiation of Notoungulata

Archaeogaia macachaae represents a new mammalian taxon for the Mealla Fm. The presence of a disto-lingual cingulid that runs mesially from the hypoconulid to the mesial face of the entoconid (147^0), recovered here as an autapomorphy of *Archaeogaia*, plus the small size of m3 reinforce its recognition as a new genus and species. On the other hand, the lower molars of *Archaeogaia macachaae* present a trigonid with short mesio-distal protolophid, transverse metalophid and mesio-distal hypolophid slightly convex labially (ch. 54^1), and an entoconid transversely expanded into entolophid (55^1), traits that support its inclusion within the order Notoungulata. Nevertheless, this new taxon fluctuates its location within the order as indicated by the reduced consensus (Fig. 5B). These oscillations are inferred to be associated to the fact that *Archaeogaia* is only known by its m1-3; that it shows plesiomorphic features, such as the presence of brachydont cheek teeth (ch. 20^0), and a faint mesial lophid (paralophid?) in a paraconid position on its lower cheek teeth (ch. 53^0) (see Appendix 3, Supplementary data), and that it lacks several features that define other

notoungulate groups (e.g., characters 58 and 65 to 68). It is worth mentioning that it never clusters with *Simpsonotus* spp. (*S. praecursor* and *S. major*), the only other notoungulate – and mammal– genus known for the Mealla Fm.

Notwithstanding the phylogenetic affinities of *Archaeogaia*, and considering the age of the Mealla Fm. (Ca. 63.49-59.23 Ma.), it is clear to us that the Notoungulata from this unit in Salta (*Archaeogaia*) and Jujuy (*Simpsonotus*) provinces (e.g., Pascual et al., 1978) represent an early diversification of the group. This best matches with the hypotheses of divergence time between Notoungulata and Litopterna in the earliest Paleocene (Westbury et al., 2017; *Ca*. 65 Ma.) than in the late Cretaceous (Welker et al., 2015; 69-64 Ma.). Unfortunately, the Paleocene mammalian record of Notoungulata is scarce, only represented by an indeterminate henricosborniid from the Santa Lucía Fm. at Tiupampa locality in Bolivia (Muizon et al., 2019), which is slightly younger than the records mentioned above. The following record of a notoungulate corresponds to *Perutherium*, from the probably late Paleocene-early Eocene Lower Muñani Fm. at Laguna Umayo locality in Peru (Sigé et al., 2004). *Satshatemnus* from the Río Loro Fm., Tucumán Province (Soria and Powell, 1981) could be an additional late Paleocene-early Eocene record for the Order Notoungulata. Since the record of Notoungulata from low and middle latitudes is scarce, the necessity of paleontological prospections proved to be essential, particularly in the Salta Group.

VI. Conclusion

The present study describes a new genus and species from the early-middle Paleocene of Northwestern Argentina: *Archaeogaia macachaae* gen. et sp. nov. A phylogenetic analysis nests this taxon within Notoungulata due to the shared synapomorphies (presence of a transverse entolophid, and lower cheek teeth with short mesio-distal protolophid, transverse metalophid, and mesio-distal hypolophid slightly convex labially). *Archaeogaia*

macachaae is diagnosed by the following combination of features: small size, brachydont dentition, m1 slightly shorter than m2 and both larger than m3; talonid slightly lower than trigonid, being similar in width in m2, but narrower in m3; metaconid slightly higher than the protoconid and distally placed; reduced, but conspicuous paraconid that is located in the mesial wall of the metalophid; straight metalophid which runs mesially forming a slightly obtuse angle in the labial edge of the m2, whereas it forms a right angle with the longitudinal axis of the tooth in m3; m2-3 with mesio-lingual cingulid; and a continuous disto-lingual cingulid that extends from the hypoconulid to the mesial face of the entoconid, being less developed in the area between the entoconid and the metaconid, this cingulid is particularly conspicuous in m3.

Archaeogaia improves the knowledge of the Notoungulata from the Paleocene of the Northwestern Argentina, previously represented by the single genus *Simpsonotus*, and together, they constitute the oldest record of Notoungulata from South America (Ca. 63.49-59.23 Ma.). The age of the latter reinforces the hypotheses based on molecular data that argue Paleocene age for the split of Notoungulata and Litopterna.

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VIII. References

Ameghino, F., 1901. Notices préliminaires sur les ongulés nouveaux des terrains crétacés de Patagonie. Boletín de la Academia Nacional de Ciencias de Córdoba, 16, 348–426.

Bauzá, N., Gelfo, J.N., López, G.M., 2019. Early steps in the radiation of notoungulate mammals in southern South America: A new henricosborniid from the Eocene of Patagonia. Acta Palaeontologica Polonica, 64, 597–607.

Billet, G., 2011. Phylogeny of the Notoungulata (Mammalia) based on cranial and dental characters. Journal of Systematic Paleontology, 9, 481–497. http://dx.doi.org/10.1080/14772019.2010.528456.

Billet, G., Muizon, C. 2013. External and internal anatomy of a petrosal from the late Paleocene of Itaborai, Brazil, referred to Notoungulata (Placentalia). Journal of Vertebrate Paleontology, 33, 455–469.

Bond, M., 1981. Un nuevo Oldfieldthomasiidae (Mammalia, Notoungulata) del Eoceno Inferior (Fm. Lumbrera, Grupo Salta) del NW argentino. In: II Congreso Latinoamericano de Paleontología, Porto Alegre, 2, 521–536.

Bond, M., Carlini, A. A., Goin, F. J., Legarreta, L., Ortiz-Jaureguizar, E.,

Pascual, R., Uliana, M. A., 1995. Episodes in South American land mammal evolution and sedimentation: Testing their apparent concurrence in a Paleocene succession from central Patagonia. In: VI Congreso Argentino de Paleontología y Bioestratigrafía, Trelew, 1, 47–58.

Bown, T. M., Kraus, M. J., 1979. Origin of the tribosphenic molar and metatherian and eutherian dental formulae. In: Lillegraven, J. A., Kielan-Jaworowska, Z., Clemens, W. A. (Eds.), Mesozoic Mammals: The First Two-thirds of Mammalian History. University of California Press, Berkeley, California, 172–181.

Bremer, K., 1994. Branch support and tree stability. *Cladistics*, 10, 295–304.

Calle, A. Z., Horton, B. K., Limachi, R., Stockli, D. F., Uzeda-Orellana, G. V., Anderson, R. B., Long, S. P., 2018. Cenozoic provenance and depositional record of the Subandean foreland basin during growth of the central Andean fold-thrust belt, southern Bolivia. In: Zamora Valcarce, G., McClay, K., Ramos, V. A. (Eds.), *Petroleum Basins and Hydrocarbon Potential of the Andes of Peru and Bolivia*. American Association of Petroleum Geologists Memoir, 117, 483–530.

Carrillo, J. D., Asher, R. J., 2017. An exceptionally well-preserved skeleton of *Thomashuxleya externa* (Mammalia, Notoungulata), from the Eocene of Patagonia, Argentina. Palaeontologia Electronica, 20.2.34A, 1–33 http/:palaeo-electronica.org/content/2017/1930-anatomy-and-systematics-of-thomashuxleya-externa-notoungulata

Chornogubsky, L., Goin, F. J., 2015. A review of the molar morphology and phylogenetic affinities of *Sillustania quechuense* (Metatheria, Polydolopimorphia, Sillustaniidae), from the early Paleogene of Laguna Umayo, southeastern Peru, Journal of Vertebrate Paleontology. http://dx.doi.org/10.1080/02724634.2015.983238

Cifelli, R., 1983. The Origin and Affinities of the South American Condylarthra and Early Tertiary Litopterna (Mammalia). American Museum Novitates, 2772, 1–49.

Clyde, W. C., Wilf, P., Slingerland, R. L., Barnum, T., Bijl, P. K., Bralower, T. J., Brinkhuis, H., Comer, E. E., Huber, B. T., Ibanez-Mejia, M., Jicha, B. R., Krause, J. M., Schueth, J. D., Singer, B. S., Raigemborn, M. S., Schmitz, M. D., Sluijs, A., Zamaloa, M., 2014. New age constraints for the Salamanca Formation and lower Rio Chico Group in the western San Jorge Basin, Patagonia, Argentina: implications for Cretaceous–Paleogene extinction recovery and land mammal age correlations. Geological Society of America Bulletin, 126, 289–306. http://dx.doi.org/10.1130/B30915.1

Comer, E., Slingerland, R. L., Krause, J.M., Iglesias, A., Clyde, W.C., Raigemborn, M.S., Wilf, P., 2015. Sedimentary facies and depositional environments of diverse early Paleocene floras, north-central San Jorge basin, Patagonia, Argentina. Palaios, 30, 553–573.

Croft, D., Gelfo, J.N., López G.M., 2020. Splendid Innovation: The Extinct South American Native Ungulates. Annual Review of Earth and Planetary Sciences, 48, 11–32.

De Celles, P., Horton, B. K., 2003. Early to Middle Tertiary foreland development and the history of Andean crustal shortening in Bolivia. Geological Society of America Bulletin, 115, 58–77.

del Papa, C.E., 2006. Estratigrafía y Paleoambientes de la Formación Lumbrera, Grupo Salta, Noroeste Argentino. Revista Asociación Geológica Argentina, 61, 15–29.

del Papa, C. E., Kirschbaum, A., Powell, J. E., Brod, A., Hongn, F., Pimentel, M., 2010. Sedimentological, geochemical and paleontological insights applied to continental omission surfaces: a new approach for reconstructing an Eocene foreland basin in NW Argentina. Journal of South American Earth Sciences, 29, 327–345.

Demouy, S., Paquette, J. L., de Saint Blanquat, M., Benoit, M., Belousova, E. A., O´Reilly, S. Y., García, F., Tejada, L. C., Gallegos, R., Sempere, T., 2012. Spatial and temporal evolution of Liassic to Paleocene arc activity in southern Peru unraveled by zircon U-Pb and Hf in-situ data on plutonic rocks. Lithos, 155, 183–200. http://dx.doi.org/10.1016/j.lithos.2012.09.001.hal-00756611.

Deraco, V., García-López, D. A., 2016. A new Eocene Toxodontia (Mammalia, Notoungulata) from northwestern Argentina, Journal of Vertebrate Paleontology, 36, 1, e1037884. http://dx.doi.org/10.1080/02724634.2015.1037884

Garcia-López, D.A., 2011. Basicranial osteology of Colbertia lumbrerense Bond, 1981 (Mammalia: notoungulata). *Ameghiniana*, 48, 3–13.

García-López, D. A., Powell, J., 2009. Un nuevo Oldfieldthomasiidae (Mammalia, Notoungulata) del Paleógeno de la provincia de Salta, Argentina. Ameghiniana, 46, 153–164.

Gelfo, J., Goin, F., Woodburne, M., Muizon, C., 2009. Biochronological relationships of the earliest South American Paleogene mammalian faunas. Paleontology, 52, 251–269.

Gelfo, J.N., García-López, D.A., Bergqvist, L.P., 2020. Phylogenetic relationships and palaeobiology of a new xenungulate (Mammalia: Eutheria) from the Palaeogene of Argentina, Journal of Systematic Palaeontology, https://doi.org/10.1080/14772019.2020.1715496

Goloboff, P. A., 1999. Analyzing large data sets in reasonable times: solutions for composite optima. Cladistics, 15, 415–428.

Goloboff, P. A., Catalano, S. A., 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics, http://dx.doi.org/10.1111/cla.12160

Gómez Omil, R. J., Boll, A., Hernández, R. M., 1989. Cuenca cretácico-terciaria del Noroeste argentino (Grupo Salta). In Chebli, G. A. and Spalletti, L. A. (Eds.), Cuencas Sedimentarias Argentinas. Universidad Nacional de Tucumán, Serie de Correlación Geológica. Tucumán, 43–64.

Hooker, J.J., 1986. Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England. Bulletin of British of Natural History (Geol.), 39, 191–478.

Horton, B. K., 2018. Sedimentary record of Andean mountain building. Earth-Science Reviews, 178, 279–309.

Horton, B.K., Hampton, B.A., Waanders, G., 2001. Paleogene synorogenic sedimentation in the Altiplano plateau and implications for initial mountain building in the central Andes: Geological Society of America Bulletin, 113, 1387–1400.

Hyland, E., Sheldon, N., Cotton, J., 2015. Terrestrial evidence for a two-stage mid-Paleocene biotic event. Palaeogeography Palaeoclimatology Palaeoecology, 417, 371–378.

Hyland, E., Sheldon, N., Cotton, J., 2017. Constraining the early Eocene climatic optimum: a terrestrial interhemispheric comparison. Geological Society American Bulletin, 129, 244–252.

Hyland, E., Sheldon, N., 2018. Comment on “Paleosol-based paleoclimate reconstruction of the Paleocene-Eocene Thermal Maximum, northern Argentina” by Andrews, E., White, T., and del Papa, C. [Palaeogeography, Palaeoclimatology, Palaeoecology, 471, 181–195]. Palaeogeography, Palaeoclimatology, Palaeoecology, 511, 639–642.

Krause, M. J., Clyde, W. C., Ibañez-Mejía, M., Schmitz, M. D., Barnum, T., Bellosi, E., Wilf, P., 2017. New age constraints for early Paleogene strata of central Patagonia, Argentina: Implications for the timing of South American Land Mammal Ages. Geological Society of America Bulletin, 129, 886–903. http://dx.doi.org/10.1130/B31561.1

Legarreta, L., Uliana, M., 1994. Asociaciones de fósiles y hiatos en el Supracretácico-Neógeno de Patagonia: una perspectiva estratigráfico-secuencial. Ameghiniana, 31, 257–281.

López, G.M., Gelfo, J.N., Bauzá, N., Bond, M., Tejedor, M.F., 2020. Biochron and diversity of Archaeopithecidae (Mammalia, Notoungulata) and a new genus and species from the Eocene of Patagonia, Argentina. Ameghiniana, http://dx.doi.org/10.5710/AMGH.18.01.2020.3291

Madden, R.H., Carlini, A.A., Vucetich, M.G., Kay, R.F., 2010. The Paleontology of Gran Barranca. Evolution and Environmental Change through the Middle Cenozoic of Patagonia. Cambridge University Press, New York, 460 pp.

Marquillas, R., del Papa, C., Sabino, I., 2005. Sedimentary aspects and paleoenvironmental evolution of a rift basin: Salta Group (Cretaceous-Paleogene), northwestern Argentina. International Journal of Earth Sciences, 39, 489–516.

Marquillas, R.A., Salfity, J.A., Matthews, S. J., Matteini, M., Dantas, E., 2011. U-Pb zircon age of the Yacoraite Formation and its significance to the Cretaceous-Tertiary boundary in the Salta basin, Argentina. In: Salfity, J.A., Marquillas, R. A. (Eds), Cenozoic Geology of the Central Andes of Argentina. SCS publisher, Salta, 225–244.

Marshall, L.G., Sempere, T., Butler, R. F., 1997. Chronostratigraphy of the mammal-bearing Paleocene of South America. Journal of South American Earth Sciences, 10, 49–70.

Moreno, J. A., 1970. Estratigrafía y paleogeografía del Cretácico superior en la cuenca del noroeste argentino, con especial mención de los subgrupos Balbuena y Santa Bárbara. Revista de la Asociación Geológica Argentina, 24, 9–44.

Muizon de, C., 1991. La fauna de mamíferos de Tiupampa (Paleoceno inferior, Formación Santa Lucia), Bolivia. Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos, 1, 575–624.

Muizon de, C., Billet, G., Argot, C., Ladevèze, S., Goussard, F., 2015. *Alcidedorbignya inopinata*, a basal pantodont (Placentalia, Mammalia) from the early Palaeocene of Bolivia: anatomy, phylogeny and palaeobiology. Geodiversitas, 37, 397–634.

Muizon de, C., Billet, G., Ladevèze, S., 2019. New remains of kollpaniine "condylarths" (Panameriungulata) from the early Palaeocene of Bolivia shed light on hypocone origins and molar proportions among ungulate-like placentals. Geodiversitas, 41, 841–874. https://doi.org/10.5252/geodiversitas2019v41a25.

Ogg, J. G., 2012. The Geomagnetic Polarity Timescale. In: Gradstein, F. M., Ogg, J. G., Schmitz, M. D., Ogg, G.M. (Eds.), The Geologic Time Scale 2012. Elsevier, 85–113.

Ortiz-Jaureguizar, E., Pascual, R., 2011. The tectonic setting of the Caribbean region and the K/T turnover of the South American land-mammal fauna. Boletín Geológico y Minero, 122, 333–344.

Ortiz-Jaureguizar, E., Cladera, G., Giallombardo, A., 1999. Relaciones de similitud entre las faunas del lapso Cretácico superior-Paleoceno superior en América del Sur. Temas Geológico-Mineros, 26, 280–283.

Palma, R. M., 1984. Características estratigráficas y sedimentológicas de las formaciones en el límite Cretácico-Terciario inferior en la Cuenca Salteña. PhD thesis, Universidad Nacional de Tucumán.

Pascual, R., Bond, M., Vucetich, M. G., 1981. El subgrupo Santa Bárbara (Grupo Salta) y sus vertebrados; cronologia, paleoambientes y paleobiogeografía. In: VIII Congreso Geológico Argentino, Buenos Aires, 8, 743–758.

Pascual, R., Vucetich, M. G., Fernández, J., 1978. Los primeros mamíferos (Notoungulata, Henricosborniidae) de la Formación Mealla (Grupo Salta, subgrupo Santa Bárbara). Sus implicancias filogenéticas, taxonómicas y cronológicas. Ameghiniana, 15, 366–390.

Pascual, R., Ortiz-Jaureguizar, E., 2007. The Gondwanan and South American episodes: two major and unrelated moments in the history of the South American mammals. Journal of Mammalian Evolution, 14, 75–137.

Paula Couto, C. de., 1979. Tratado de Paleomastozoología. Academia Brasileira de Ciências, 596.

Paula Couto, C., 1952. Fossil mammals from the beginning of the Cenozoic in Brazil. Condylarthra, Litopterna, Xenungulata and Astrapotheria. Bulletin of American Museum

of Natural History, 99, 355–394.

Price, L. I., Paula Couto, C. de., 1950. Vertebrados terrestres do Eoceno na bacia calcárea de ltaboraí, Brasil. In: XX Congresso Panamericano Engenharia de Minas e Geologia, Rio de Janeiro, 149-173.

Quattrocchio, M., Volkheimer, W., del Papa, C., 1997. Palynology and paleoenvironments of the 'Faja Gris', Mealla Formation (Salta Group) at Garabal Creek (NW Argentina). Palynology, 21, 231–247.

Quattrocchio, M., Volkheimer, W., 2000. Paleoclimatic changes during the Paleocene-Eocene in the Salta Group Basin, NW Argentina. In: Volkheimer, W., Smelka, A. (Eds.), Southern Hemisphere Paleo- and Neoclimates: Key Sites, Data, and Models. Springer, New York, 353–367.

Raigemborn, M.S., Krause, J.M., Bellosi, E., Matheos, S.D., 2010. Redefinición estratigráfica del Grupo Río Chico (Paleógeno inferior), en el norte de la cuenca del Golfo San Jorge, Chubut, Argentina. Revista de la Asociación Geológica Argentina, 67, 239–256.

Raigemborn, M.S., Beilinson, E., 2020. Stratigraphic architecture and paleosols as basin correlation tools of the early Paleogene infill in central–south Patagonia, Golfo San Jorge Basin, Argentinean Patagonia. Journal of South American Earth Sciences, http://dx.doi.org/10.1016/j.jsames.2020.102519

Rak, A. J., McQuarrie, N., Ehlers, T. A., 2017. Kinematics, exhumation, and

sedimentation of the north central Andes (Bolivia): An integrated thermochronometer and thermokinematic modeling approach. Tectonics, 36, http://dx.doi.org/10.1002/2016TC004440

Roth, S., 1903. Noticias preliminares sobre nuevos mamíferos fósiles del Cretáceo superior y Terciario inferior de la Patagonia. Revista del Museo de La Plata, 11, 133–158.

Salfity, J.A., Marquillas, R.A., 1994. Tectonic and sedimentary evolution of the Cretaceous–Eocene Salta Group Basin, Argentina. In: Salfity, J. A. (Ed), Cretaceous tectonics in the Andes, Earth Evolution Sciences Monograph Series, Wiesbaden, Germany, 266–315.

Sempere, T., Butler, R. F., Richards, D. R., Marshall, L. G., Sharp, W., Swisher III, C. C., 1997. Stratigraphy and chronology of Upper Cretaceous–lower Paleogene strata in Bolivia and northwest Argentina. Geological Society of America Bulletin, 109, 709–727.

Sigé, B., Sempere, T., Butler, R. F., Marshall, L. G., Crochet, J-Y., 2004. Age and stratigraphic reassessment of the fossil bearing Laguna Umayo red mudstone unit, SE Peru, from regional stratigraphy, fossil record and paleomagnetism. Geobios, 37, 771–793.

Simpson, G. G., 1935. Occurrence and relationships of the Río Chico fauna of Patagonia. American Museum Novitates, 818, 1–21.

Simpson, G.G., 1948. The Beginning of the Age of Mammals in South América. Part 1. Introduction. Systematics: Marsupialia, Edentata, Condylarthra, Litopterna and Notioprogonia. Bulletin of the American Museum of Natural History, 91, 1-232.

Simpson, G.G., 1967. The beginning of the age of mammals in South America. Part 2. Systematics : Notoungulata, concluded (Typotheria, Hegetotheria, Toxodonta, Notoungulata incertae sedis), Astrapotheria, Trigonostylopoidea, Pyrotheria, Xenungulata, Mammalia incertae sedis. Bulletin of the American Museum of Natural History, 137, 1–260.

Soria, M. F., Powell, J. E., 1981. Un primitivo Astrapotheria (Mammalia) y la edad de la Formación Río Loro, Provincia de Tucumán, República Argentina. Ameghiniana, 18, 155–168.

Sprain, C.J., Renne, P.R., Wilson, G.P., Clemens, W.A., 2015. High-resolution chronostratigraphy of the terrestrial Cretaceous-Paleogene transition and recovery interval in the Hell Creek region, Montana. Geological Society of America Bulletin, 127, 393–409. http://dx.doi.org/10.1130/B31076.1

Starck, D., 2011. Cuenca Cretácica-Paleógena del Noroeste Argentino. In: VIII Congreso de Exploración y Desarrollo de Hidrocarburos Simposio Cuencas Argentinas: visión actual, Mar del Plata, 1, 407–453.

Vera, B., 2012. Revisión del género Transpithecus Ameghino, 1901 (Notoungulata, Interatheriidae) del Eoceno medio de Patagonia, Argentina. Ameghiniana, 49, 60 – 74.

Welker, F., Collins, M. J., Thomas, J. A., Wadsley, M., Brace, S., Cappellini, E., Turvey, S. T., Reguero, M., Gelfo, J. N., Kramarz, A., Burger, J., Thomas-Oates, J, Ashford, D. A., Ashton, P. D., Rowsell, K., Porter, D. M., Kessler, B., Fischer, R., Baessmann, R., Kaspar, S., Olsen, J. V., Kiley, P., Elliott, J. A., Kelstrup, C. D., Mullin, V., Hofreiter, M., Willerslev,

E., Hublin, J. J., Orlando, L., Barnes, I., MacPhee, R. D. E., 2015. Ancient proteins resolve the evolutionary history of Darwin´s South American ungulates. Nature, http://dx.doi.org/10.1038/nature14249.

Westbury, M., Baleka, S., Barlow, S., Hartmann, S., Paijmans, J. L. A., Kramarz, A., Forasiepi, A. M., Bond, M., Gelfo, J. N., Reguero, M. A., López-Mendoza, P., Taglioretti, M., Scaglia, F., Rinderknecht, A., Jones, W., Mena, F., Billet, G., Muizon, C., Aguilar, J. L., MacPhee, R. D. E., Hofreiter, M., 2017. A mitogenomic timetree for Darwin´s enigmatic South American mammal Macrauchenia patachonica. Nature Communications, 8, 15951, http://dx.doi.org/10.1038/ncomms15951.

White, T., del Papa, C., Andrews, E., 2018. Chronostratigraphy of Paleogene strata, Salta Basin, northwestern Argentina: A reply to Hyland and Sheldon's comment. Palaeogeography, Palaeoclimatology, Palaeoecology, 511, 643–645.

Williamson, T. E., Brusatte, S. L., Carr, T. D., Weil, A., Standhardt, B. R., 2012. The phylogeny and evolution of Cretaceous–Palaeogene metatherians: cladistic analysis and description of new early Palaeocene specimens from the Nacimiento Formation, New Mexico. Journal of Systematic Palaeontology, 10, 625–651.

Wilkinson, M., 1994. Common cladistic information and its consensus representation: Reduced Adams and Reduced Cladistic Consensus Trees and Profiles. Systematic Biology, 43, 343–368.

Wilkinson, M., 1995. Coping with abundant missing entries in phylogenetic inference using parsimony. Systematic Biology, 44, 501–514.

Wilkinson, M., 2001. Phylogenetic Analysis. In: Briggs, D. E. G., Crowther, P. R. (Eds.) Palaeobiology II. Blackwell, Oxford, 509–515.

Woodburne, M. O., Goin, F. J., Bond, M., Carlini, A. A., Gelfo, J. N., Lopez, G. M., Iglesias, A., Zimicz, A. N., 2014. Paleogene land mammal faunas of South America: a response to global climatic changes and indigenous floral diversity. Journal of Mammalian Evolution, 21, 1–73. http://dx.doi.org/10.1007/s10914-012-9222-1.

Figure Captions

Figure 1 [2 column]. A, sedimentary log of the Mealla Fm. outcrop at Tonco Valley with the magnetic polarity zonation modified from Hyland et al. (2015) after White et al. (2018); **B**. geographic location of Tonco Valley, Salta Province, northwestern Argentina.

Figure 2 [2 column]. Late Cretaceous-late Eocene time scale showing South American mammalian biochronological units. Age, Epoch, Stage and Polarity Chron follow Ogg (2012). Age of the Mealla Fm. follows White et al. (2018). Age of Santa Lucía Fm. follows Sempere et al. (1997). Age of the Patagonian units follows Krause et al. (2017). Black circles represent the known isotopic dates based on: Marquillas et al. (2011) (Yacoraite Fm.); Sempere et al. (1997) (El Molino Fm.); del Papa et al. (2010) (upper section of Lumbrera Fm.). Stratigraphy of Bolivia follows De Celles and Horton (2003) and Horton (2018); northwestern Argentina follows White et al. (2018); partially del Papa et al. (2010). Black squares represent magnetostratigraphic dates following White et al. (2018) (Mealla

Formation). Question signs represent uncertainties in the age of the boundaries. Arrows in the South American mammalian assemblages column highlight the location of northwestern Argentina faunas. Age of Paso del Sapo fauna follows Tejedor et al. (2009). Age of Laguna Umayo fauna after Sigé et al. (2004). Bones represent the mammal-bearing levels.

Figure 3 [1,5 column]. *Archaeogaia macachaae* gen et sp. nov. **A**, occlusal view of the specimen IBIGEO-P73 partial left mandible with m1-3. **B**, labial view. **C**, enlarged view of the m2. **D**, enlarged view of the m3. **Abbreviations**. **co**, cristid oblicua; **dc**, distal cingulid; **dist**, distal; **ecfd**, ectoflexid; **ed**, entoconid; **elf**, entolofid; **hld**, hypoconulid; **hlf**, hypolophid; **lab**, labial; **ling**, lingual; **mes**, mesial; **mlf**, metalophid; **mc**, mesial cingulid; **mes**, mesial; **pad**, paraconid; **palf**, paralophid; **prlf**, protolophid; **v.dis.tal.,** talonid distal valley; **v.mes.tal.**, talonid mesial valley. Scale: 1 mm.

Figure 4 [1,5 column]. *Archaeogaia macachaae* gen et sp. nov. **A**, occluso-lingual view of the m2. **B**, occlusal view of the m3. **Abbreviations**. see Figure 3. Scale: 1 mm.

Figure 5 [2 column]. Phylogenetic analysis. A, strict consensus of 6104 most parsimonious trees of 423 steps (CI=0.295; RI=0. 650). B, reduced consensus showing the diverse positions *Archaeogaia* in all the MPTs. The numbers above and below nodes represent the Bremer and Bootstrap (left, absolute; right, GC frequencies) supports, respectively. In bold, node numbers.

Table 1. Measurements in mm of IBIGEO-P 73. * indicate a measurement was estimated measuring the length of the fracture on the m1 and resting this value to the tooth length.

Tooth	Length	Trigonid Width	Talonid Width	Trigonid Height	Talonid Height
m1	**4,10***	**2,34**	**2,10**	**2,24**	**2,23**
m2	**4,19**	**2,49**	**2,52**	**2,21**	**2,04**
m3	**3,55**	**2,30**	**1,85**	**2,31**	**1,78**
Relative length					
m2/m1	**1,02**	**m3/m1**	**0,87**	**m2/m3**	**1,18**
Relative area					
m2/m1	**1,09**	**m3/m1**	**0,85**	**m2/m3**	**1,27**
Relative length of molars respect the total molar row					
m1	**0,35**	**m2**	**0,35**	**m3**	**0,30**

Figure 1 [2 columns]

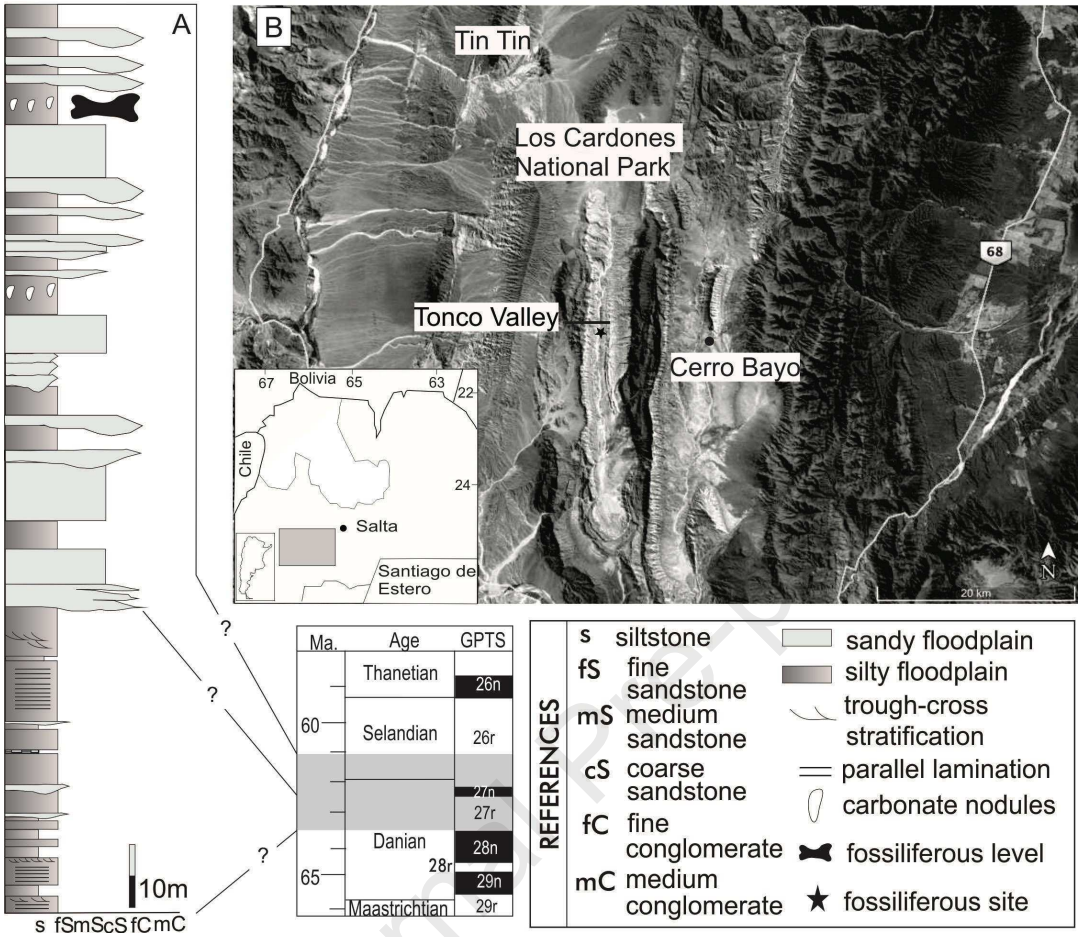


Figure 2 [2 columns]

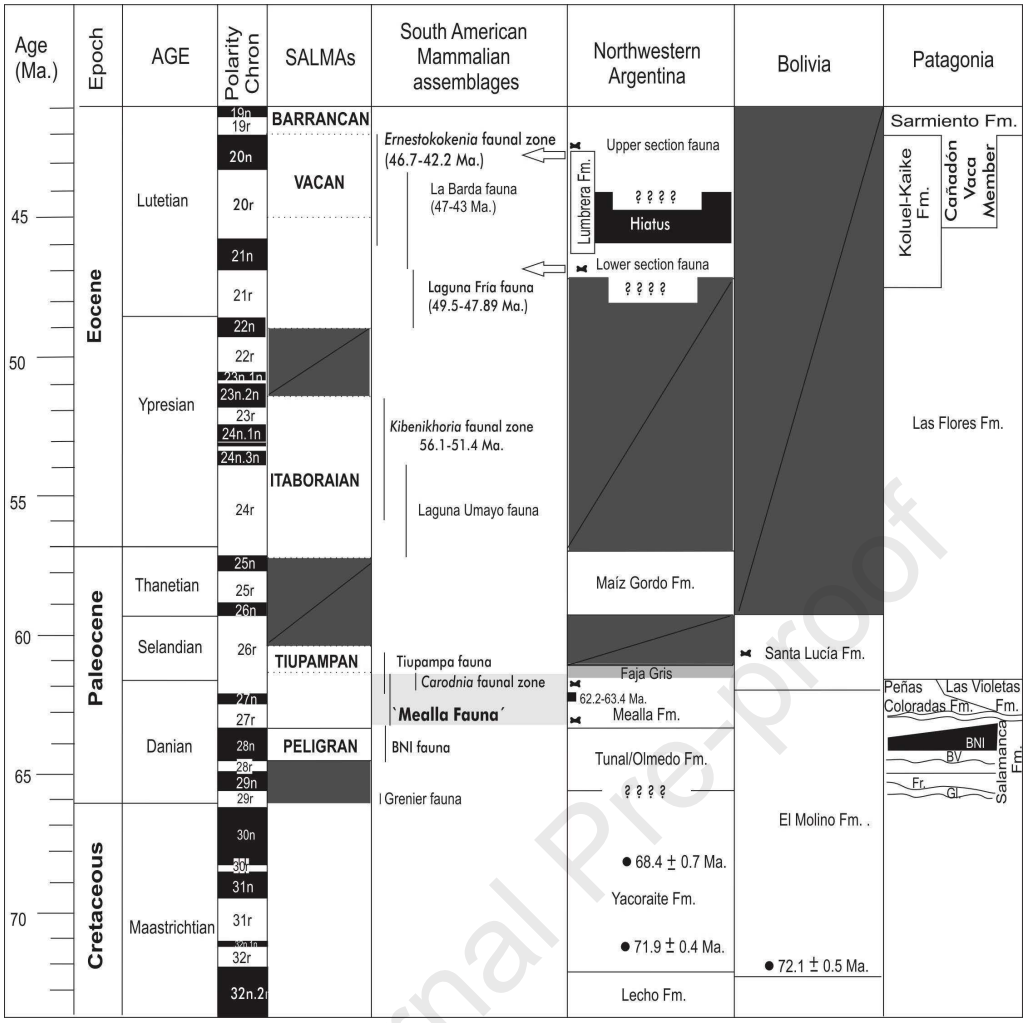


Figure 3 [1,5 columns]

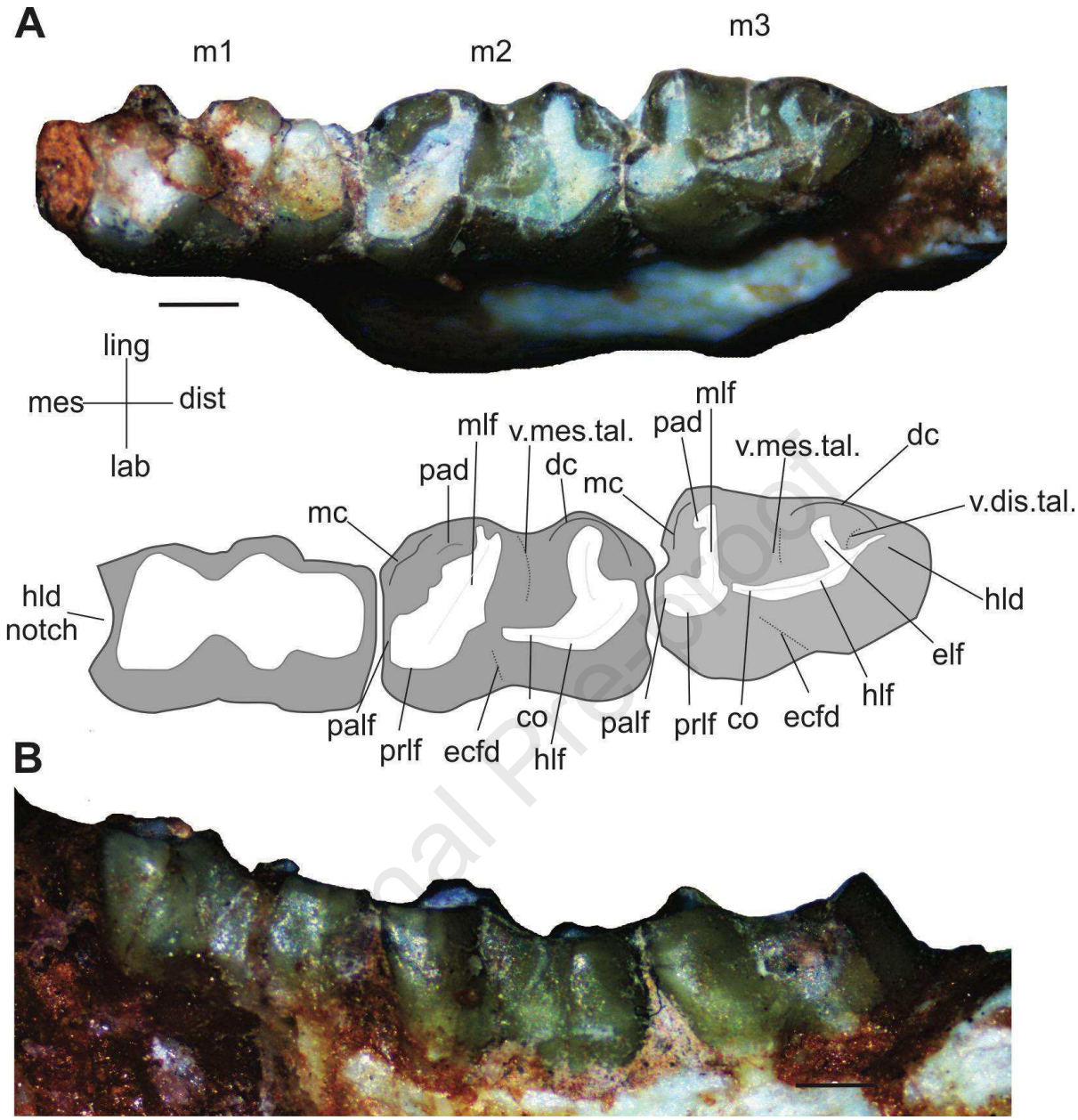


Figure 4 [1,5 columns]

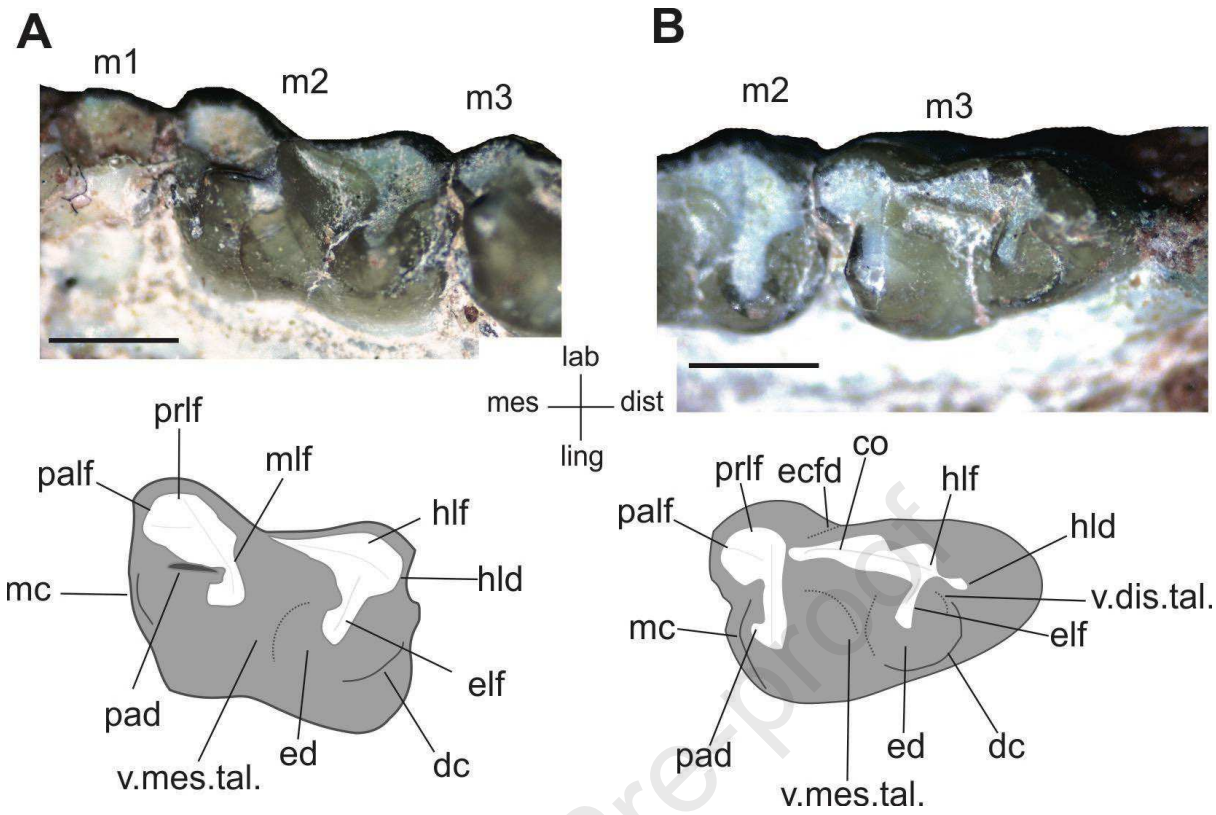
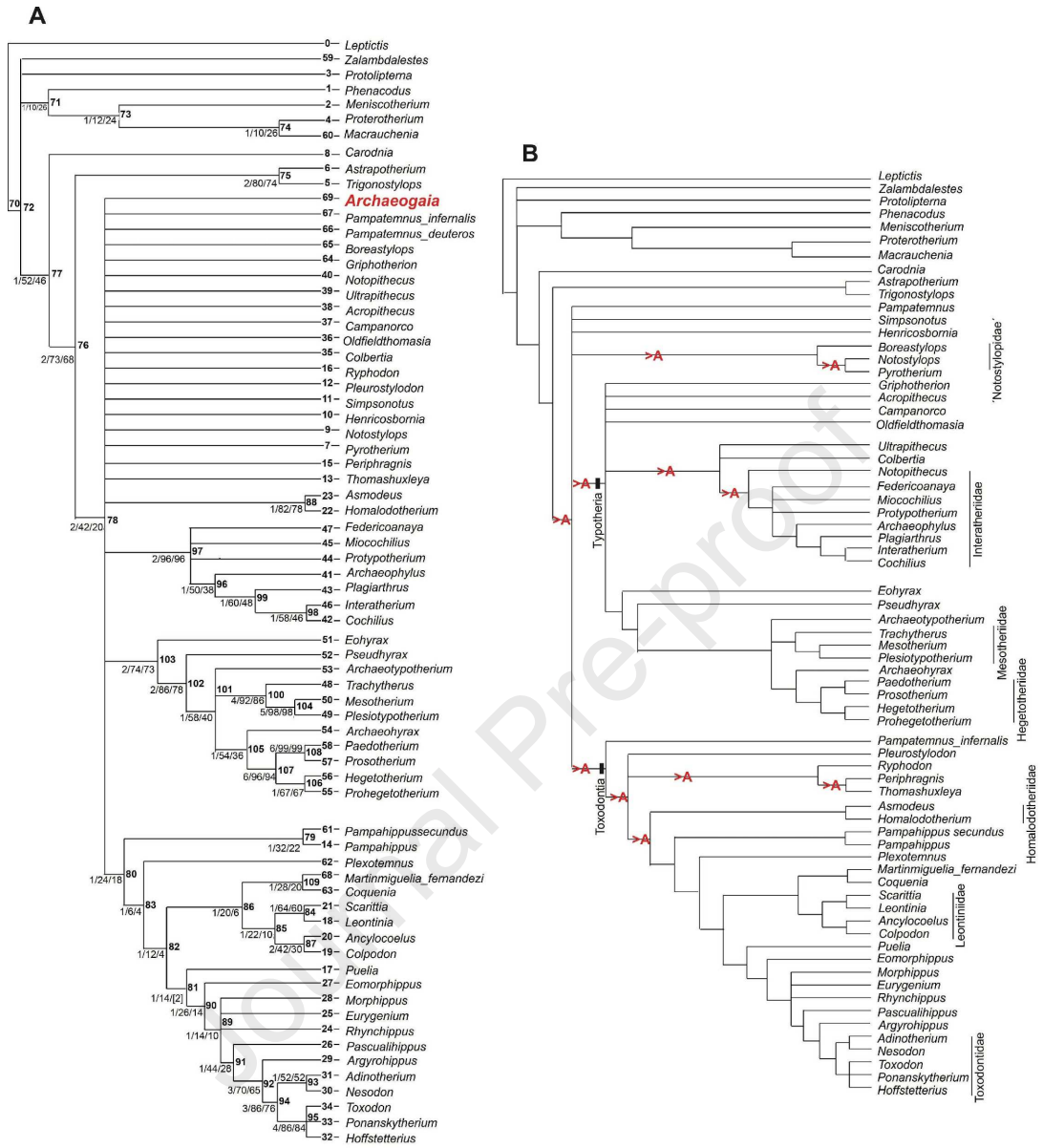


Figure 5 [2 columns]



Highlights

1. A new genus and species (*Archaeogaia macachaae)* is described within order Notoungulata, the most diverse clade of South American native ungulates.
2. This new taxon comes from the upper levels of the Mealla Formation (late Danian-early Selandian, Salta Group), and constitutes the second mammalian taxa known for this unit.
3. Together with *Simpsonotus* spp., this finding constitutes the most ancient record for the order Notoungulata.
4. These new finding reinforces the necessity of new paleontological prospections in the Paleocene of the Northwestern Argentina, particularly in the Salta Group.

AUTHORSHIP STATEMENT

Manuscript title:

"Archaeogaia macachaae gen. et sp. nov., one of the oldest Notoungulata Roth, 1903 from the early-middle Paleocene Mealla Formation (Central Andes, Argentina) with insights into the Paleocene-Eocene South American biochronology"

All persons who meet authorship criteria are listed as authors, and all authors certify that they have participated sufficiently in the work to take public responsibility for the content, including participation in the concept, design, analysis, writing, or revision of the manuscript. Furthermore, each author certifies that this material or similar material has not been and will not be submitted to or published in any other publication before its appearance in the Hong Kong Journal of Occupational Therapy.

Authorship contributions
Please indicate the specific contributions made by each author (list the authors' initials followed by their surnames, e.g., Y.L. Cheung). The name of each author must appear at least once in each of the three categories below.

Category 1
Conception and design of study: NZ, MF, MB, LC, JCF
acquisition of data: NZ, MF, MB
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Category 2
Drafting the manuscript: NZ, MF, MB, LC, MA, MC, JCF
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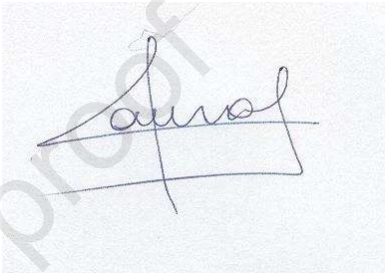
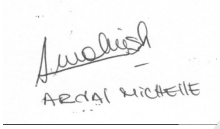
Laura Chornogubsky 6-17-2020 

Michelle Arnal  6-17-2020

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Conflicts of Interest

Archaeogaia macachaae gen. et sp. nov., one of the oldest Notoungulata Roth, 1903 from the early-middle Paleocene Mealla Formation (Central Andes, Argentina) with insights into the Paleocene-Eocene South American biochronology

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☐ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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